PSYCHE

Vol. 62 March, 1955 No. 1

HEALED WOUNDS AND GALLS ON FOSSIL LEAVES FROM THE WILCOX DEPOSITS (EOCENE) OF WESTERN TENNESSEE

By H. K. Brooks

University of Cincinnati, Cincinnati, Ohio

Introduction

The specimens described herein are not the first evidence of insects to be reported from the Eocene deposits of Western Tennessee and the adjoining states of Alabama, Mississippi, Arkansas and Kentucky. Features produced by the activities of insects on fossil leaves have been described and figured by Berry (1916, 1928, 1930, and 1931). Collins (1925, p. 406) observes that "Insects must have been more or less plentiful at this time, as we find such evidence of them as fossil insect galls and caddis fly tubes, while leaves occasionally exhibit holes, galleries and irregular margins which are due in all probability to insect ravages."

The alleged evidence of insect activities, a termite wing described by Collins (1925), a wing of a large ponerine ant by Carpenter (1929) and the elytra of three species of beetles by Wickham (1929) are the only traces of arthropods reported from the Wilcox deposits of Tennessee and adjoining states. These deposits have yielded one of the best preserved early Tertiary floras of North America and it seems anomalous that arthropods should have left such a meager record.

The caddis fly cases constructed of fragments of leaves are well preserved and have been well illustrated by Berry

(1928). With the exception of the galls, the other alleged insect-produced features have either been misinterpreted or the features are of questionable significance.

Collection and Occurrence

The specimens described below were collected by the late Dr. R. Lee Collins. They are from a clay lens in the Holly Springs formation exposed in a clay pit immediately southwest of Puryear, Henry County, Tennessee. This lens of kaolinitic clay contains an abundance of well preserved angiosperm leaves. Berry (1916 and 1930) studied the flora and determined the age of the deposit to be lower Eocene.

Berry (1928, p. 3) interpreted the paleoecology of these deposits of crossbedded sands and lenses of plant bearing clays to be nonmarine. "The general environmental picture of this area during the time of deposition . . ., is of a low, abundantly forested, warm temperate coast, with bayou-like stream distributaries emptying into lagoons ponded behind extensive barrier beaches, beyond which the gulf waters were extremely shallow, and not typically marine for a considerable distance."

Evidence of Leaf-cutting Bees

In 1916, Berry (p. 33, pl. 107, fig. 5) figured a leaf of *Icacorea prepaniculata* from Puryear, Tennessee, which he states is "badly riddled in a manner suggesting the work of leaf-cutting bees." The figured specimen has over sixty small, irregular holes. This is not the type of injury produced by recent megachilid bees and therefore Berry's alternate suggestion that the holes "are due to a brood of leaf-eating caterpillars" is a better guess. Later, Berry (1930, pl. 48, fig. 33) figured a leaflet of *Cassia fayettensis* from the same locality with a very irregular saw-toothed margin. Small notches variable in size but all less than 2 mm. across have been cut-out all around its margin. The explanation of the figure states that it is "A leaflet showing an insect-cut margin," and it is cited (Berry, 1931, p. 302) as "a specimen which has been cut in a manner which may indicate the work of some lower Eocene leaf-cutting bee." In the same paper, a leaf of *Icacorea* *perpaniculata* from Graves County, Kentucky, with embayments cut into its margins, 6 to 9 mm. across, is figured and discussed. The notches are crudely semicircular and are variable in outline and in size. Berry admits the dubious nature of these injuries and suggests as an alternative that the cuts may have been made by caddis fly larvae for the construction of cases.

These examples are all suggestive of the work of leaf-eating insects. The last specimen cited may have been cut by a primitive leaf-cutting bee, the work of which appears cruder than that of the modern Megachilidae but can hardly be regarded as conclusive evidence of the presence of megachilid bees in the Eocene forest of Tennessee and adjoining states.

A bee-cut *Nectandra pseudocoriacea* leaf, more authentic than those described by Berry, was collected by R. Lee Collins at Puryear, Tennessee. The leaf has four semicircular pieces, 5 to 6 mm. in diameter, cut from one of its edges (pl. 1, fig. 1 and 1a). The darkened borders of the wounds appear to be lignitized remains of scar tissue. Recent female megachilid bees inflict similar injuries in cutting pieces of leaves for the construction of nests. Semicircular pieces are cut for the construction of the sides and circular pieces for partitions. In contrast, damages to leaves produced by phytophagous insects are irregular in shape. The scar tissue proves that the leaf remained on the tree for some time after it was injured and could not have been cut by a caddis fly larva for pieces of leaves to construct a case (pl. 1, fig. 6) as Berry suggested (1931, p. 303). The uniformity of the shape and size of the injuries and the presence of the scar tissue is credible evidence that the fossil leaf was damaged by a leaf-cutting bee.

No fossil Megachilidae have been reported from rocks older than the Oligocene deposits of Florissant, Colorado (Cockerell, 1908). The deposit has also yielded a leaf with semicircular notches cut into its margin which Cockerell (1910, p. 429) states is evidence that the habit of cutting out pieces of leaves for building nests was as highly developed by the megachilid bees during the Oligocene as it is at present. On the basis of the above described insect-cut leaf, the range of the Megachilidae is provisionally extended to the Eocene.

Leaves Damaged by Phytophagous Insects

Nearly half of the extant species of insects are phytophagous (Brues, 1946, p. 90) and phytophagy is generally assumed to be the primitive diet. It is perplexing, therefore, that no example of the remains of fossil plants from the Paleozoic and lower and middle Mesozoic have been reported exhibiting healed wounds that could have been caused by insects. However, most Recent defoliators feed on angiosperms and healed damages are rather common on fossil angiosperm leaves from the Cretaceous and Tertiary.

A variety of healed injuries which appear to be due to phytophagous insects are shown on leaves figured on plate 1, fig. 2, fig. 4, fig. 5, and fig. 7. Determination of the culprits responsible for the different types of damage is impossible.

The "galleries" in the angiosperm leaves from the Wilcox deposits mentioned and figured by Berry (1916, p. 32; pl. 23, fig. 3; pl. 31, fig. 1 and fig. 3; pl. 38, fig. 4; pl. 39, and pl. 92) and which were later referred to by Collins (1925, p. 406) are not the same as the meandering, elongate, narrow wounds surrounded by scar tissue on the portion of a *Proteoides wilcoxensis* leaf shown enlarged in fig. 5.

Explanation of Plate 1

Figure 1. A fossil leaf, *Nectandra pseudocoriacea* Berry, from the Wilcox deposits of Puryear, Tennessee, bearing injuries inflicted by megachilid bees. Figure 1a. A portion of the above described leaf enlarged to twice natural size to show the scar tissue surrounding the injuries. Figure 2. A fossil leaf, *Nectandra pseudocoriacea* Berry, bearing healed wounds probably inflicted by defoliating phytophagous insects. Figure 3. A fossil leaf, *Cupanites formosus* Berry, bearing simple pouch galls. Figure 4. A fossil leaflet, *Cassia sp.*, bearing healed wounds. Figure 5. A portion of a fossil leaf, *Proteoides wilcoxensis* Berry, enlarged four times to show healed meandering wounds. Figure 6. Fossil caddis fly case, *Folindusia wilcoxiana* Berry, found in association with the other figured specimens. Figure 7. A fossil leaf, *Nectandra pseudocoriacea* Berry, badly damaged by leaf-eating insects and bearing 11 galls. Figure 7a. A portion of figure 7 enlarged 10 times to show one of the galls.

Brooks — Fossil Galls

These wounds were inflicted by some creature crawling on the surface of the leaf and not by a mining insect, such as the larvae of some moths and saw flies which tunnel through mesophyll.

This author has seen nothing suggestive of the activity of leaf mining insects on fossil leaves. The "galleries" referred to appear to be products of preservation as they consist of low ridges of uniform width which run across the leaves irrespective of the veins and the midribs.

Galls

Traumatic plant growths comparable to Recent galls are uncommon on the remains of plants from Tertiary. Fossil galls have been figured from the Wilcox deposits of Tennessee by Berry (1916, p. 33, pl. 56, fig. 2, and pl. 111, fig. 1), mentioned by Collins (1925, p. 406) and again by Berry (1931, p. 301). Scudder (1886, p. 98) mentions cynipid galls from the Oligocene deposits of Florissant, Colorado and a gall was figured, discussed and named by Cockerell (1908, p. 66, pl. 5, fig. 7) and Brues (1910, p. 14, fig. 7). The Oligocene galls were later discussed by Kinsey (1919, p. 44-49) and he states that they are synonyms and definitely are not cynipid galls. Miocene galls from Douglas County, Washington, have been described by Hoffman (1932, p. 341-342, fig. 1) and compared to Recent cynipid and itonid galls. Brues (1946, p. 171) mentions that galls have been observed on Cretaceous leaves but does not document his statement.

The leaf of *Cupanites formosus* illustrated on plate 1, fig. 3 from Puryear, Tennessee, has many malformations between the veins and veinlets which closely resemble Recent simple pouch galls. The individual irregular pouches average about 1 mm. in diameter and vary from about one-half to twice this size. The individual pouches are simple invaginations from the ventral side of the leaf. Similar Recent homeomorphic abnormalities are commonly produced on leaves by gall mites (Eriophyidae), aphids (Aphidae), jumping plant lice (Chermidae=Psyllidae) and several other types of lowly arthropods. Crinkling of leaves which bears some resemblance to the malformations on the fossil leaf are sometimes produced by fungal infections.

Not only does the leaf of *Nectandra pseudocoriacea* figured on plate 1, fig. 7, bear the results of the activity of some leaf-eating organism, presumably an insect, but the remaining part of the leaf bears eleven well preserved "cone" galls (fig. 7a). The structures are mammilliform and seem to be separated from the leaf by a constriction at the point of attachment. They are elliptical at the base, 1 mm. by 0.8 mm., and taper to a blunt apex about 0.4 mm. above the surface of the leaf. Immediately surrounding the galls, the leaves are darkened. The darkened areas probably reflect sclerotized leaf tissue in the vicinity of the galls as the coloration is due to a greater amount of lignitized leaf residue.

These "cone" galls are comparable in size and general shape to some Recent galls induced to develop on leaves by gall mites (Eriophyidae), plant lice (Phylloxeridae) and especially by gall midges (Cecidomyiidae=Itonididae) and by gall wasps (Cynipidae). The sclerotized leaf tissue surrounding the galls is suggestive of Recent "leaf spot galls" produced by the gall midge, *Cecidomyia ocellaris* on maple leaves (Felt, 1940, fig. 258).

Neither of the alleged insect galls described and figured by Berry (1916, pl. 111, fig. 1, and pl. 56, fig. 2) is similar to the structures described above. One consists of small, deep, conical depressions on the impression of a leaf and the other is a compression of a petiole gall. Both figured specimens seem to bear authentic galls.

Though binomial names have been proposed by Cockerell (1908) and Brues (1910) for fossil galls, it is believed that no useful purpose is served by naming such objects.

Gall forming arthropods are small and fragile and thus there is an extremely meager fossil record of their remains. The reported stratigraphic ranges of the families mentioned above are as follows:

Class Arachnida

Order Acarina, Family Eriophyidae, no fossils

Class Insecta

Order Hemiptera, Family Phylloxeridae, no fossils

Family Chermidae, Oligocene to Recent (Handlirsch, 1921).

Family Aphidae, Cretaceous (?) to Recent (Essig, 1937).

Order Diptera, Family Cecidomyiidae, Eocene? to Recent (Handlirsch, 1921).

Order Hymenoptera, Family Cynipidae, Cretaceous (?) to Recent (Kinsey, 1937).

ACKNOWLEDGEMENTS

Dr. Frank M. Carpenter kindly provided information on the known stratigraphic ranges of the families mentioned. Dr. Roland W. Brown identified the fossil leaves and made several helpful suggestions and corrections on a preliminary copy of this paper.

It is hoped that this paper will be a tribute to the late Dr. R. Lee Collins who recognized the significance of these fossils. They have been placed in the collections of the United States National Museum where many other excellent specimens of fossil plants from the Wilcox deposit collected by Dr. Collins have previously been placed.

LITERATURE CITED

BERRY, E. W.

1916. The Lower Eocene floras of southeastern North America: U.S. Geol. Survey, Prof. Pap. 91.

1928. A new type of caddis case from the Lower Eocene of Tennessee: U.S. Nat. Mus. Proc., **71**: art. 14.

1930. Revision of the Lower Eocene Wilcox flora of the southeastern states, with descriptions of new species from Tennessee and Kentucky: U.S. Geol. Survey, Prof. Pap. 156.

1931. An insect-cut leaf from the Lower Eocene: Am. Jour. Sci., **21**: 301-304.

BRUES, C. T.

1910. The parasitic Hymenoptera of the Tertiary of Florissant, Colorado: Bull. Mus. Comp. Zool., **54**: 1-125.

1946. Insect dietary: Harvard Univ. Press, Cambridge, Mass.

CARPENTER, F. M.

1929. A fossil ant from the Lower Eocene (Wilcox) of Tennessee: Jour. Wash. Acad. Sci., **19**: 300-301.

COCKERELL, T. D. A.

1908. Fossil insects from Florissant, Colorado: Am. Mus. Nat. Hist., **24**: 59-69.

1908. A fossil leaf-cutting bee (*Megachile praedicta,* Florissant, Colo.): Canadian Entomologist, **40**: 31-32.

1910. A Teritiary leaf-cutting bee: Nature, **82**: 429.

Collins, R. L.

1925. A Lower Eocene termite from Tennessee: Am. Jour. Sci., ser. 5. **9**: 406-410.

Essig, E. O.

1937. Insects and Arachnids from Canadian Amber: Univ. Toronto Studies, Geol. Ser., **40**:18.

Felt, E. P

1940. Plant galls and gall makers: Comstock Pub. Co., Ithaca, N.Y.

Handlirsch, A.

1921. Palaeontologie: In Schröder's Handbuch der Entomologie, **3**: 206-213; 274-283.

Hoffman, A.

1932. Miocene insect gall impressions: Bot. Gazette, **93**: 341-342.

Kinsey, A. C.

1919. Fossil Cynipidae: Psyche, **26**: 44-49.

1937. Insects and Arachnids from Canadian Amber: Univ. Toronto Studies, Geol. Ser., **40**: 21.

Scudder, S. H.

1886. Systematic review of fossil insects: U.S. Geol. Survey Bull., **31**.

Wickham, H. F.

1929. Coleoptera from the Lower Eocene (Wilcox) clays: Jour. Washington Acad. Sci., **19**: 149-150.